

A Revision of the Recent Species of *Eudolium* Dall, 1889 (Gastropoda: Tonnoidea)

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ABSTRACT

The tonnid genus *Eudolium* contains three Recent species: *E. crosscanum* Monterosato, 1869 (= *thompsoni* McGinty, 1955), *E. bairdii* Verrill & Smith (= *solidior* Dautzenberg & Fischer, 1906 = *lineata* Schepman, 1909 = *inflatum* Kuroda & Habe, 1952 = *kuroharai* Azuma, 1960) and *E. pyriforme* Sowerby, 1914. *Eudolium crosscanum* and *E. pyriforme* respectively have amphiatlantic-Mediterranean and Indo-Pacific distributions, while *E. bairdii* occurs widely in the Atlantic, Pacific and Indian Oceans. Genus and species group synonymies and distributions are discussed, and shells, radulae and male external anatomies are illustrated.

Key words: Mollusca; prosobranch gastropods; Tonnidae; *Eudolium*; systematics; zoogeography.

INTRODUCTION

The taxonomy of the species of the prosobranch family Tonnidae is poorly understood. Atlantic species were revised by Turner (1948), but there has been no critical modern revision of the Indo-Pacific species. The present contribution is the result of an attempt to determine the identity of two species of the genus *Eudolium* Dall, 1889 obtained off New Zealand in recent years.

Since Dall's (1889a) review, *Eudolium bairdii* (Verrill & Smith, 1881) has been treated as a synonym of *E. crosscanum* (Monterosato, 1869) by the majority of authors. From examination of numerous specimens, however, it transpires that not only are they distinct species, but that five subsequently introduced taxa are synonyms. Moreover, *E. crosscanum* is more closely related to the Indo-Pacific *E. pyriforme* (Sowerby, 1914) than to *E. bairdii*.

ABBREVIATIONS AND TEXT CONVENTIONS

AMS—Australian Museum, Sydney.
MCZ—Museum of Comparative Zoology, Harvard.
MNHN—Muséum National d'Histoire Naturelle, Paris.
NMNZ—National Museum of New Zealand, Wellington.
NMP—Natal Museum, Pietermaritzburg.
USNM—National Museum of Natural History, Washington, DC.

In captions to illustrations shell height dimension precedes diameter.

SYSTEMATICS

Class Gastropoda
Superfamily **Tonnoidea** Suter, 1913
Family **Tonnidae** Suter, 1913
Genus *Eudolium* Dall, 1889

Doliopsis Monterosato, 1872 (not Vogt, 1852, nor Conrad, 1865):
8. Type species (by monotypy): *Dolium crosscanum* Monterosato, 1869, Recent, Mediterranean.

Eudolium Dall, 1889a:232. Substitute name for *Doliopsis* Monterosato (preoccupied).

Galeodolium Sacco, 1891:4. Type species (by subsequent designation of Vokes, 1986:178): *Cassidaria mutica* Michelotti, 1861; Oligocene, Italy.

?*Tuberculodolium* Sacco, 1891:9. Type species (by subsequent designation of Vokes, 1986:178): *Eudolium antiquum* Sacco, 1890; Oligocene, Italy.

?*Simplicodolium* Sacco, 1891:13. Type species (here designated): *Pyrula fasciata* Borson, 1821; Pliocene, Italy.

Remarks: The shells of *Eudolium* species differ from those of *Tonna* Brunich, 1771 in having more narrowly tapered bases, consistently narrow, widely spaced spiral cords with narrow secondary spirals, and fine axial sculpture on all teleoconch whorls. The two groups are certainly closely related, with similar shells, radulae, jaws and external anatomies. An operculum is lacking in both groups, at least in the adults. *Eudolium* species are most commonly encountered at 200–600 m depth, while few *Tonna* species range much deeper than 50 m. Although *Eudolium* has been placed as a subgenus of *Tonna* by some authors (e.g., Dall, 1889a,b; Vredenburg, 1919; Thiele, 1929; Kilius, 1962), I prefer to treat it at generic level because of the distinctive shell facies and deeper center of bathymetric distribution.

As here interpreted the genus *Eudolium* contains three Recent species: *E. crosscanum* (Monterosato, 1869), *E. bairdii* (Verrill & Smith, 1881), and *E. pyriforme* (Sowerby, 1914). Of other species that have been referred

here, *Dolium* (*Eudolium*) *verrilli* Dall, 1859 has been transferred to *Hadroocorys* Quinn, 1950 (Quinn, 1950), while *E. aulacodes* Tomlin, 1927 belongs in *Oocorys* Fischer, 1853 (Kilburn, 1956). *Parvitonna perselecta* Iredale, 1931 was referred to *Eudolium* by Kiliias (1962), but the holotype (AMS C.57790) is clearly a species of *Tonna* (*sensu stricto*). *Tonna tessellatum* (Bruguière, 1759), *T. fasciatum* (Bruguière, 1759) and *T. zonatum* (Green, 1530) were referred to *Tonna* (*Eudolium*) by Vredenburg (1919), but they too belong in *Tonna* (*sensu stricto*).

Vokes (1956) interpreted Cossmann's (1903:139) statement "types de *Galeodolium* et de *Tuberculodolium*: *E. antiquum* Sacco, *Cassid. mutica* Michelotti, d'après les types communiqués par M. Sacco" as the first valid subsequent designation of type species for *Galeodolium* and *Tuberculodolium*. Cossmann, however, inadvertently reversed the order of the "type" species and thus selected species that were not originally included (ICZN Art. 69a). Although Vokes simply corrected the order, Cossmann must be considered to have associated the names *respectively*, so it is concluded that Cossmann's selection is invalid. Accordingly, Vokes (1956) is considered to be the first subsequent designator of the type species of these taxa.

Vokes (1956) used *Galeodolium* as a subgenus of *Eudolium* for species with strong nodules and a reflexed, denticulate outer lip. The differences between the type species of *Eudolium* and *Galeodolium* (Michelotti, 1561: pl. 13, fig. 16; Sacco, 1891: pl. 1, fig. 1), however, are simply matters of degree, because *E. bairdii* exhibits a smooth morphological transition between the extremes in its infraspecific variability (see below). Placement of *Tuberculodolium* and *Simplicodolium* in synonymy is tentative pending study of the type material, which was not available to me. Judging from published photographs, the undoubtedly juvenile holotype of *Eudolium antiquum* Sacco, 1890 (Ferrero Mortara *et al.*, 1954) seems narrower than confirmed species of *Eudolium*, while the lectotype of *Pyrula fasciata* Borson, 1521 (Pavia, 1976) may be a juvenile *Tonna*. Because *Galeodolium* and *Eudolium* are regarded as synonyms, and as *Eudolium* and *Tonna* are undoubtedly confamilial, Ga-

leodoliidae Sacco, 1891 is treated as a synonym of Tonnidae Suter, 1913 (1525) (Tonnidae is conserved using ICZN Art. 40b).

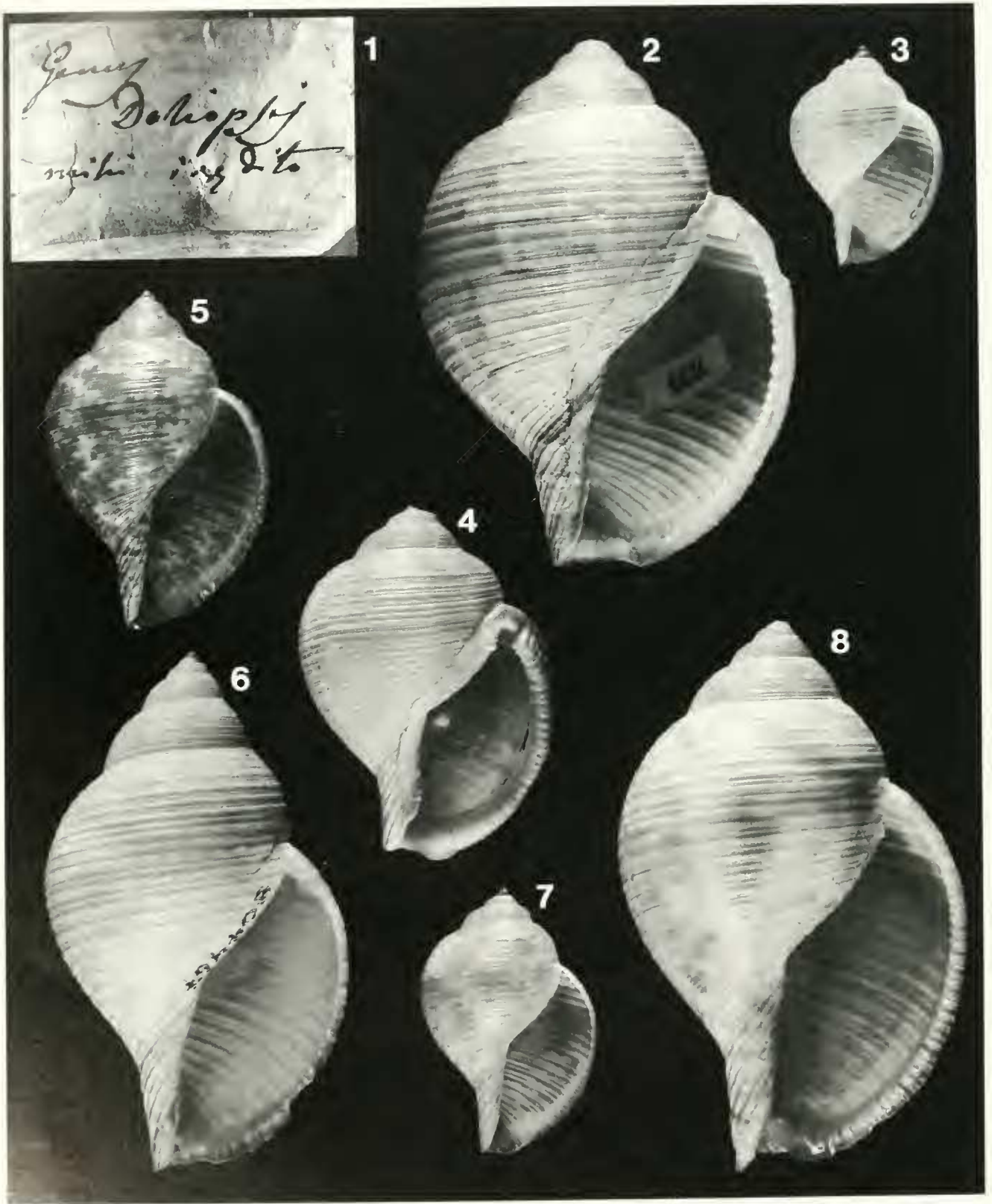
Eudolium species occur in temperate and tropical seas on soft substrata on continental shelves and slopes at 17–523 m depth. Undoubted *Eudolium* species are known from the Early Miocene [*e.g.*, *E. aoteanum* Beu, 1970] and another, unnamed species from New Zealand: *E. biornatum* (Tate, 1894) from Australia] and the Oligocene [*e.g.*, *Cassidaria mutica* Michelotti, 1561]. As with *Tonna* species (Morton, 1991) the diet consists of holothurians: the gut of a specimen of *E. bairdii* from off Mayor Island, New Zealand, contained ossicles of the apodid holothurian *Protankyra rigida* Pawson, 1965 (det. D. L. Pawson). Otherwise nothing is known of *Eudolium* biology.

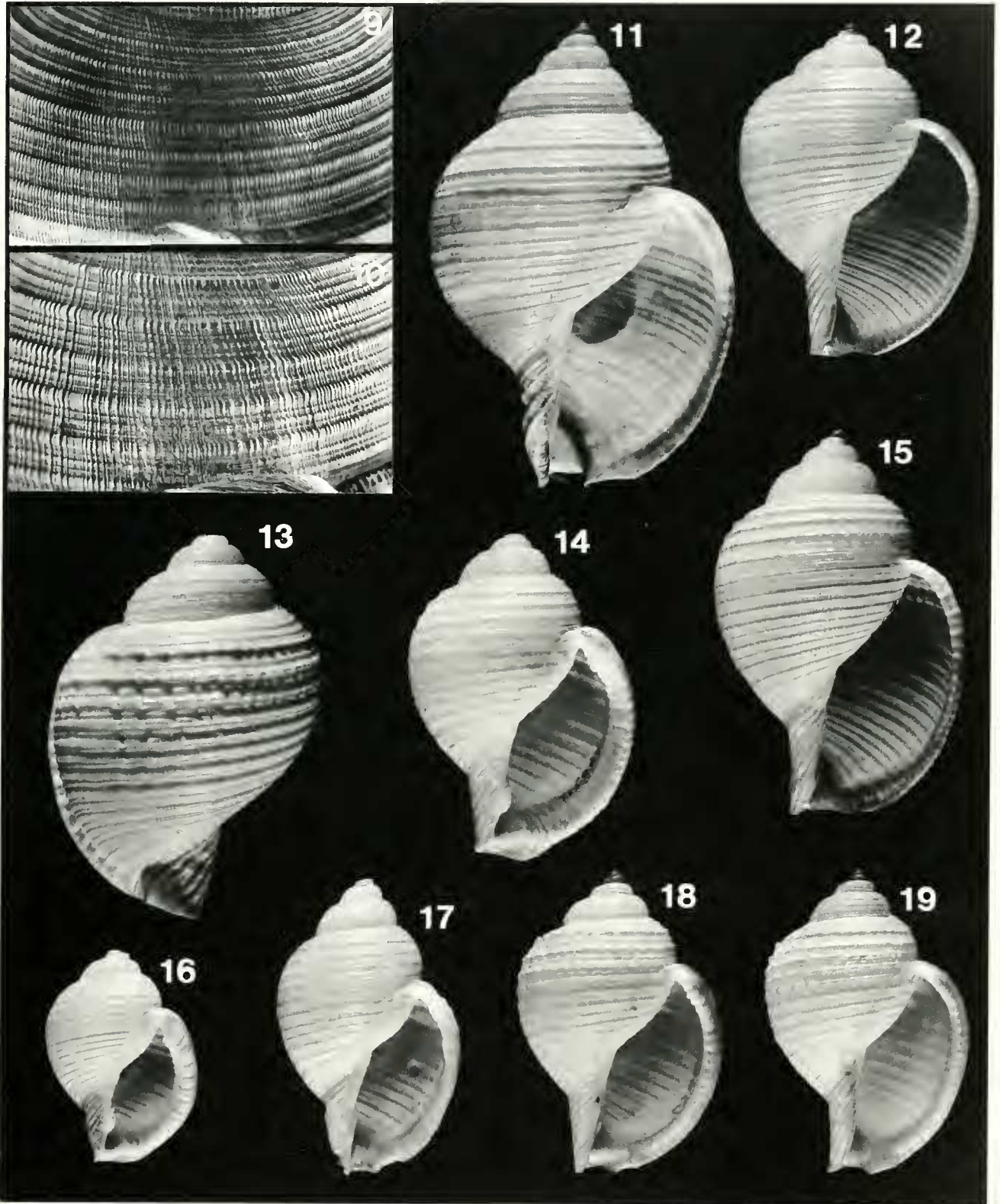
***Eudolium crosseanum* (Monterosato, 1869)**
(figures 1–4, 9, 20, 23–26, 37)

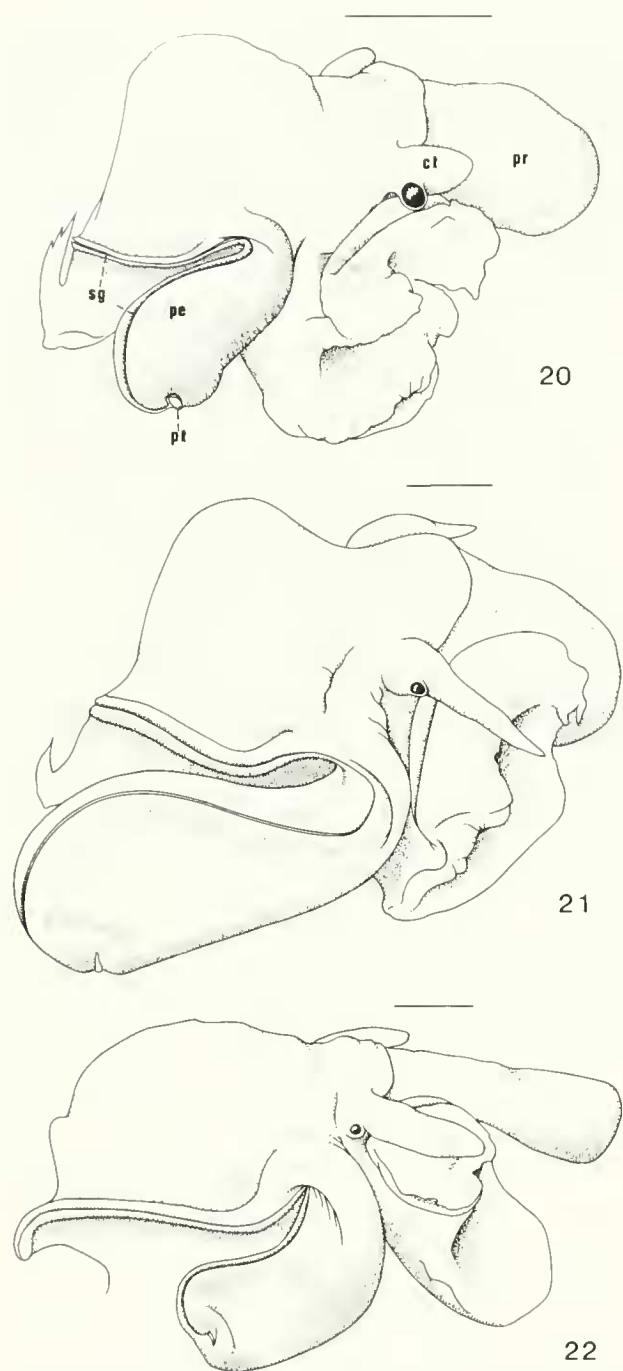
- Dolium crosseanum* Monterosato, 1869: 225, pl. 12, fig. 1; Tryon, 1855: 263, pl. 2, fig. 11 [figs. 11 and 12 transposed, fig. 12 = *D. testardi* Montrouzier, 1863].
- Doliopsis crosseana*.—Monterosato, 1872: 5, Coen, 1930: 147, figs. 1, 2 [in part—figs. 6–9 = *Galeodea echinophora* Linnaeus, 1767, P. Bouchet, personal communication].
- Dolium Eudolium crosseanum*.—Kobelt, 1905: 155, pl. 126, fig. 1 [in part—figs. 2, 3, 4 = *E. bairdii*].
- Eudolium crosseanum*.—Wenz, 1941: 1076, fig. 3066; Turner, 1945: 175 (in part—pl. 51, figs. 1, 2, text fig. 5 = *E. bairdii*).
- Eudolium testardi*.—Osima, 1943: 132, pl. 4, fig. 3 [not *Dolium testardi* Montrouzier, 1863].
- Eudolium thompsoni* McGinty, 1955: 50, pl. 1, figs. 5, 6; Abbott, 1974: 165, fig. 1755; Abbott & Dance, 1956: 119, text fig. [new synonym].
- Tonna (Eudolium) crosseana*.—Kiliias, 1962: 14, fig. 12, 6; Piani, 1977: 27, 35, figs. 3, 6, 10 [in part—fig. 5 = *Galeodea echinophora* Linnaeus, 1767, P. Bouchet, personal communication, fig. 11 = *E. bairdii*].
- Tonna (Eudolium) thompsoni*.—Kiliias, 1962: 16, fig. 12, 5.
- NOT *Dolium (Eudolium) crosseanum*.—Dall, 1859a,b; Dautzenberg & Fischer, 1906 (= *E. bairdii*).
- NOT *Dolium crosseanum*.—Locard, 1897 (*Talisman* strn. 63 = *E. bairdii*, and strn. 139 = a turrid, P. Bouchet, personal communication).

Figure 1. Label in Monterosato's handwriting gummed to dorsum of holotype of *Eudolium crosseanum*. **Figures 2–4.** *Eudolium crosseanum*. **2.** holotype, off Sicily, Hebrew University, Jerusalem No. 21356 (79.5 × 55 mm). **3.** Oregon station 3636, off Belize, USNM 751892 (32.5 × 22 mm). **4.** Oregon station 2021, off French Guiana, USNM 751855 (54 × 39.5 mm). **Figures 5–8.** *Eudolium pyriforme*. **5, 7.** Bohol Straits, Philippines, NMNZ MF. 56351 (5.51 × 34.5 mm; 7, 40.5 × 27.5 mm). **6.** David Starr Jordan station TC 40 54, off Oahu, Hawaii, USNM 504464 (79.5 × 47 mm). **8.** Southwest of Taiwan, NMNZ MF. 56350 (54.5 × 55 mm). All photographs of shells are to scale.

Figure 9. *Eudolium crosseanum*, Oregon station 3636, off Belize, USNM 751892, detail of teleoconch sculpture, 7 ×. **Figures 10–19.** *Eudolium bairdii*. **10.** detail of teleoconch sculpture, of specimen in figure 16, 7 ×. **11.** off Aldermen Islands, New Zealand, D Gibbs collection (76 × 49.5 mm). **12, 13.** off Tosa-Shimuzu, Japan, NMNZ MF.56353 (figure 12, 51 × 37 mm; figure 13, 59 × 43.4 mm). **14.** Combat station C279, Straits of Florida, USNM 715002 (49.7 × 35.5 mm). **15.** off Scot Reef, Western Australia, NMNZ MF.57427 (55 × 35 mm). **16.** Oregon II station 11133, off Yucatan Peninsula, Mexico, USNM 751930 (33 × 22.7 mm). **17.** SMIB 4 station DW55, southwest of New Caledonia, MNHN 45 × 25.5 mm. **18.** Oregon station 5690, off Colombia, USNM 751869 (46 × 31.5 mm). **19.** Albatross station 5590, Sebuku Bay, Borneo, USNM 23911 (46.5 × 31.7 mm). All photographs of whole shells are to scale.







Figures 20–22. Right lateral views of head-foot areas of male *Eudolium* animals. 20. *E. crosscanum*, Oregon station 3636, off Belize, USNM 751892. 21. *E. pyriforme*, David Starr Jordan station TC/40/54, off Oahu, Hawaii, USNM 804464. 22. *E. bairdii*, Mascareignes III station 24, off Madagascar, MNHN. Scale lines: 20 = 2.5 mm; 21, 22 = 5 mm. ct, cephalic tentacle; pe, penis; pr, proboscis; pt, penial tentacle; sg, seminal groove.

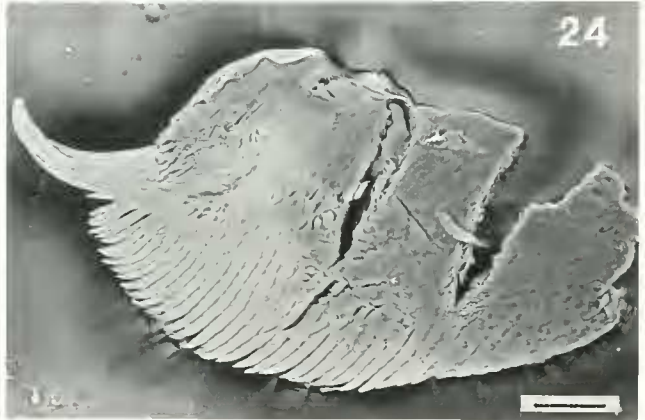
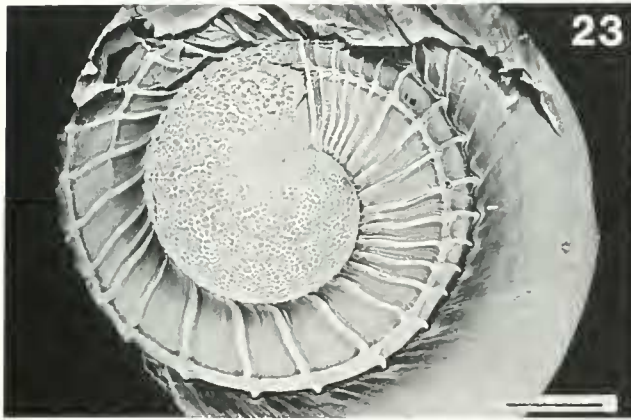
NOT *Eudolium crosscanum*.—Tomlin, 1927; Barnard, 1963; Abbott, 1974; Okutani, 1983; Kilburn, 1986; Horikoshi, 1989; Warén & Bouchet, 1990; Poppe & Goto, 1991 (= *E. bairdii*)

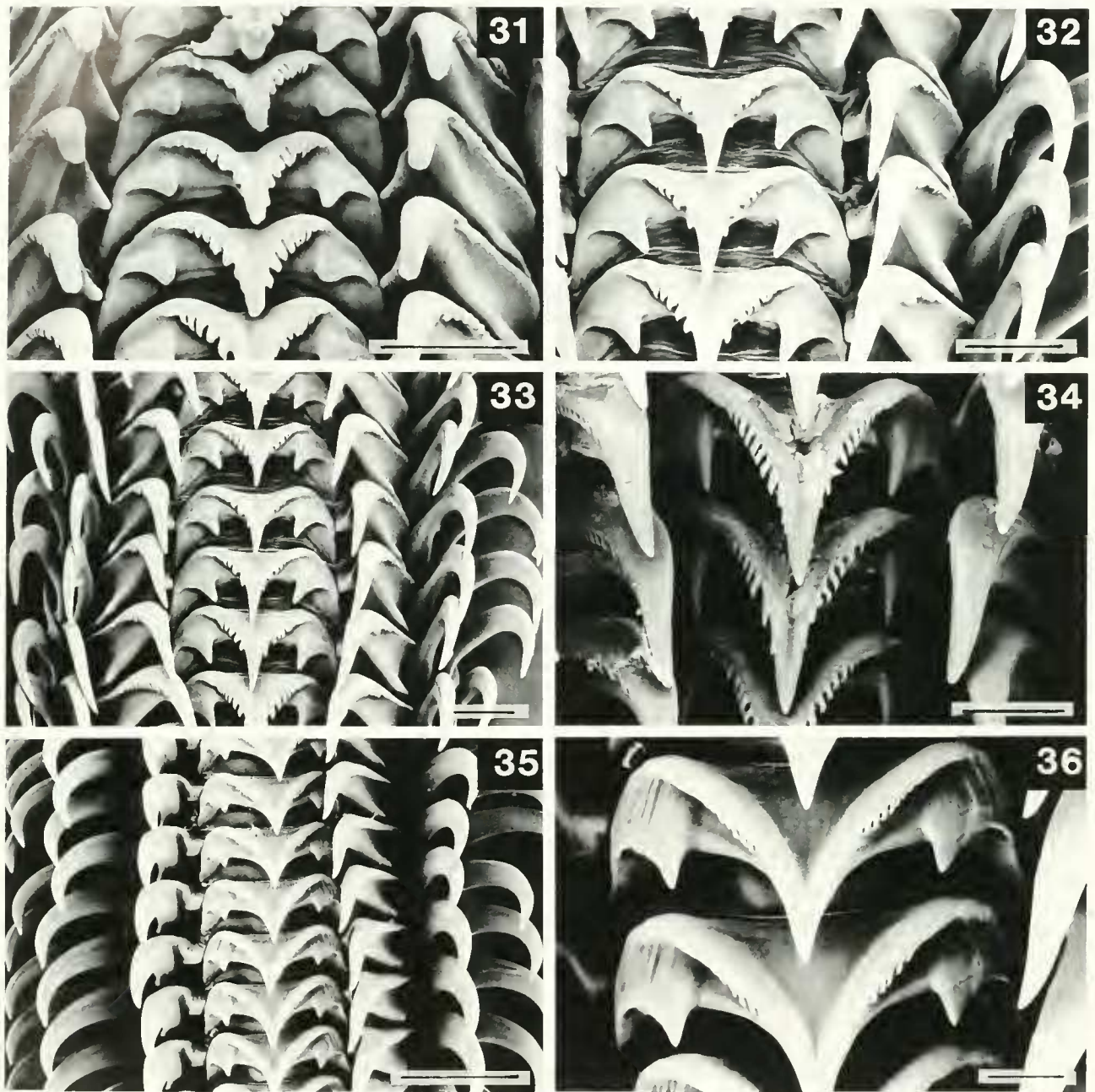
Description: Shell up to 81 mm (est.) high, thin to moderately thick, periostracum thin, straw-colored. Protoconch deep yellowish brown; teleoconch irregularly maculated with yellowish brown on a white or buff white ground, some major spiral cords with small yellowish brown spots, mature outer lip typically with a pinkish flush. Protoconch primarily conchiolin, conical, of about 5 convex whorls, 3.46–4.44 mm in diameter, sculptured with 3 rows of small periostracal spines. First whorl of calcareous mould of inner surface of protoconch (figure 23—exterior removed with sodium hypochlorite solution) 317 μm wide, sculptured with very fine irregular network of crisp threads that enclose minute, crowded, roughly circular pits. Second whorl with fine, crisp axial riblets and 2 similar crisp spiral threads, one at shoulder angulation, the other on ramp between shoulder spiral and suture. Shoulder spiral commencing immediately, ramp spiral commencing three quarters of a whorl later. Axial ribs and spiral cords becoming obsolete early on 2nd whorl. Subsequent whorls essentially smooth, rounded. Teleoconch of up to 4 evenly convex whorls, sculptured with numerous rounded spiral cords that multiply by intercalation; and fine, crisp, crowded axial riblets; in rare specimens some spiral cords becoming very weakly nodular on last adult whorl. Thin specimens with a thin, flared, weakly dentate outer lip and smooth columella and parietal area. Thickened specimens with strongly dentate outer lip, spirally plicate columella, and with 1–3 small spirally elongate denticles on parietal area close to insertion.

Animal: (figure 20: subadult male, shell height 22.3 mm, Oregon stn. 3636) Everted proboscis large, very wide but longer than broad, thin-walled. Cephalic tentacles small, slender, rounded in cross section, gently tapered, tips rounded. Eyes small, in rounded swellings on outer sides of tentacles near bases. Penis base well behind base of right cephalic tentacle, penis very large, spatulate, laterally compressed, tip broadly rounded, deeply grooved along ventral edge to tip, minute tentacle protruding from end of groove at distal extremity. Operculum absent in adults. Jaw plates (figure 24) ovate, thin, each with strong, thickened, hooked anterior projection.

Radula: (figures 25, 26) with the formula 2.1.1.1.2, teeth curved, sharply pointed, very stout, strongly interlocked. Central tooth broad; cutting area acutely angulate, 7–9 small sharp cusps on each side, terminal cusp large, long, narrow; posterolateral projections on face strong, sharp. Lateral teeth strongly longitudinally flanged along outer

Figures 23–26. *Eudolium crosscanum*. 23. protoconch with periostracum removed, Oregon station 5914, Lesser Antilles, USNM 751903. 24. (jaw plate), 25, 26. (radula) from shell 22 mm high, Oregon station 3636, off Belize, USNM 751892. 25. width of radula. 26. detail of central, lateral and marginal teeth. Figures 27–30. *Eudolium pyriforme*. Radula from shell 41 mm high, MUSORSTOM 6 station DW391, Loyalty Islands. 27. width of radula. 28–30. details of central and lateral teeth. Scale bars: 27 = 0.5 mm, others = 0.1 mm.





Figures 31–36. *Eudolium bairdii*. 31–33. radula from shell 24 mm high, Straits of Florida, Florida State Museum UF 26666. 31. detail of central and lateral teeth from anterior end of radular ribbon representing earliest teeth formed 32. detail of central, lateral and marginal teeth at posterior third of radular—note size and morphological differences compared with teeth formed earlier (31). 33. width of radula at posterior third. 34. detail of central and lateral radular teeth from shell 57 mm high, *Mascareignes III* station 24, off Madagascar, MNHN. 35, 36. radula from shell 76 mm high, off Aldermen Islands, New Zealand, D. Gibbs collection. 35. width of radula. 36. detail of central tooth. Scale bars: 35 = 0.5 mm, others = 0.1 mm.

edges to interlock with inner marginals, terminal cusp very large, 8–11 fine cusps behind on outer edge. Marginal teeth similar, without secondary cusps.

Type data: *Dolium crosseanum*: HOLOTYPE Coen collection (No. 2521), Hebrew University, Jerusalem 21386, off Palermo, Italy; *Eudolium thompsoni*: HOLOTYPE Florida State Museum, Gainesville, Florida UF

170426, Triton stn. 1206, off Sombrero Key Light, Florida Keys, 137 m.

Other material examined: WESTERN ATLANTIC—off Cape Hatteras, South Carolina, south to off French Guiana, 35°06'N–7°18'N (56 specimens in 37 lots USNM).

Distribution: (figure 37) Mediterranean and Western Atlantic, from Cape Hatteras to French Guiana; depth

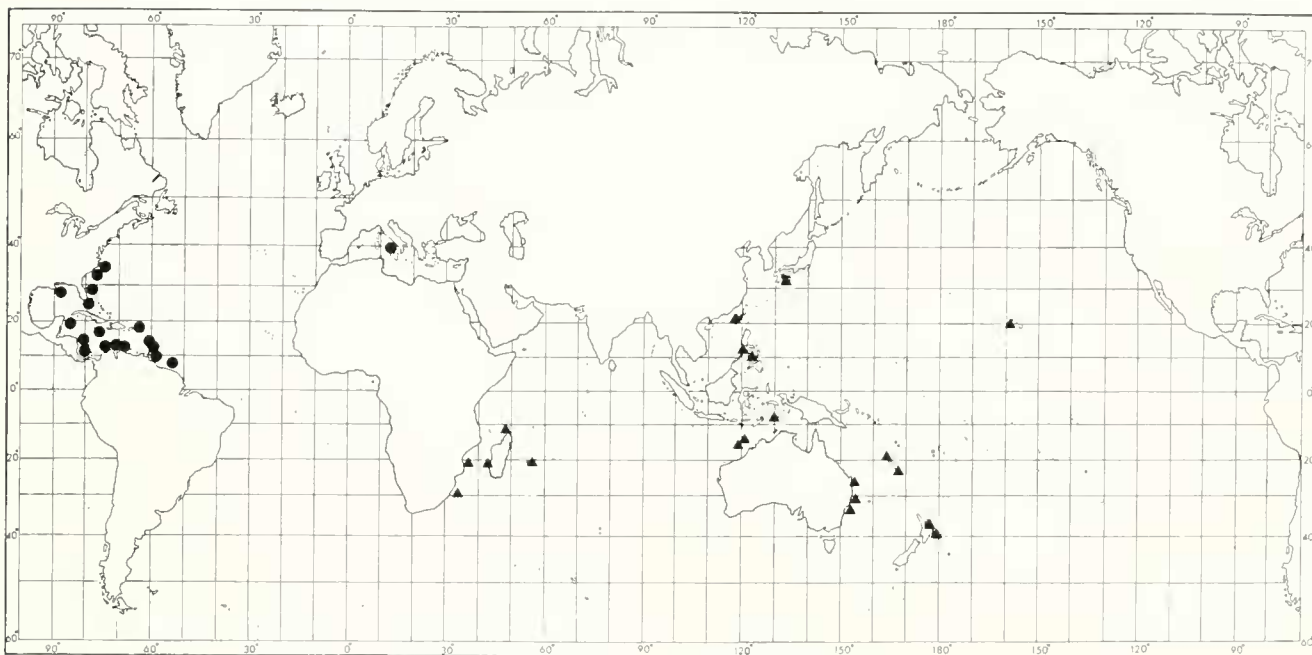


Figure 37. Map showing distribution of *Eudolium crosscanum* (●) and *E. pyriforme* (▲).

range of material examined 17–914 m, maximum known living occurrence 457 m.

Remarks: As discussed by Piani (1977) two specimens have been interpreted as the holotype of *D. crosscanum*, one in the Monterosato collection, Museo Zoologico, Roma, the other in the Coen collection, Hebrew University of Jerusalem. Piani correctly concluded that the Rome specimen cannot be the holotype because it is extensively covered by a brown periostracum and has conspicuous nodules, characters not mentioned in the rather detailed original description, and because it lacks the maculations recorded by Monterosato. From comparison of dimensions of the Rome and Jerusalem specimens with Monterosato's original published measurements, Piani (1977: 37) concluded that the Jerusalem specimen was the closest match but because there were discrepancies he suggested that it was perhaps a third example and thus by implication not the holotype. Piani (1977: figs. 6, 10) reproduced Coen's (1930: figs. 1, 2 "tipo") illustrations and a photograph (provided by H. K. Mienis) of the Jerusalem specimen. Upon receipt of the Jerusalem specimen (figures 1, 2), kindly lent to me by H. K. Mienis, it was immediately obvious that Piani's illustrations are of one and the same specimen, though this was neither unequivocally stated by Piani nor evident from the illustrations.

It transpires that the dimensions of the Jerusalem specimen were wrongly quoted by Piani (1977:37), as they in fact closely accord with Monterosato's (1869) original measurements ("long 81; diam. maj. 56 mill.; apert. 62 mill. longa, 28 lata"): height 79.8 mm (lacks protoconch—estimated height when intact 81 mm), diameter 58 mm, height of aperture 62 mm, width of aperture 28

mm. The general shell facies, color and color pattern of this specimen agree closely with the original description, while the number of denticles on the outer lip (32) are closely accordant: Monterosato stated that there were 33 denticles, but it is possible that a low swelling at the abapical extremity of the lip was also counted. The only discrepancy is the thickness of the outer lip, which ranges from 3.5 to 4.0 mm over the denticulate area, and not 3 mm as stated by Monterosato. The smooth zone at the adapical extremity, however, is 3 mm thick, suggesting that Monterosato may have measured it there to avoid including the denticles. Diagnostic features of this particular specimen that were realised on the original drawing include the distinctive pattern of chipping at the rim of the anterior siphonal canal, and the growth scar in front of the columella. Incontrovertible proof that this specimen belonged to Monterosato is the label in Monterosato's handwriting gummed to the dorsum (figure 1) "Genus Doliopsis mihi inedito".

The specific identity of the Rome specimen is uncertain, but judging from Piani's (1977: fig. 11) illustration it is much more strongly nodular than any specimen of *E. crosscanum* seen during the present study and seems more likely to be *E. bairdii* (P. Bouchet concurs). Other published records of *E. crosscanum* from the Mediterranean apart from references to the holotype are based on misidentification (see synonymy).

By direct comparison of the holotypes, the Western Atlantic *E. thompsoni* McGinty, 1955 is specifically indistinguishable from *E. crosscanum*. Judging from the fact that the species has only been obtained once in the Mediterranean yet it is relatively common in the western Atlantic, it is likely that the Mediterranean specimen is the result of a chance introduction of a teleplanic larva

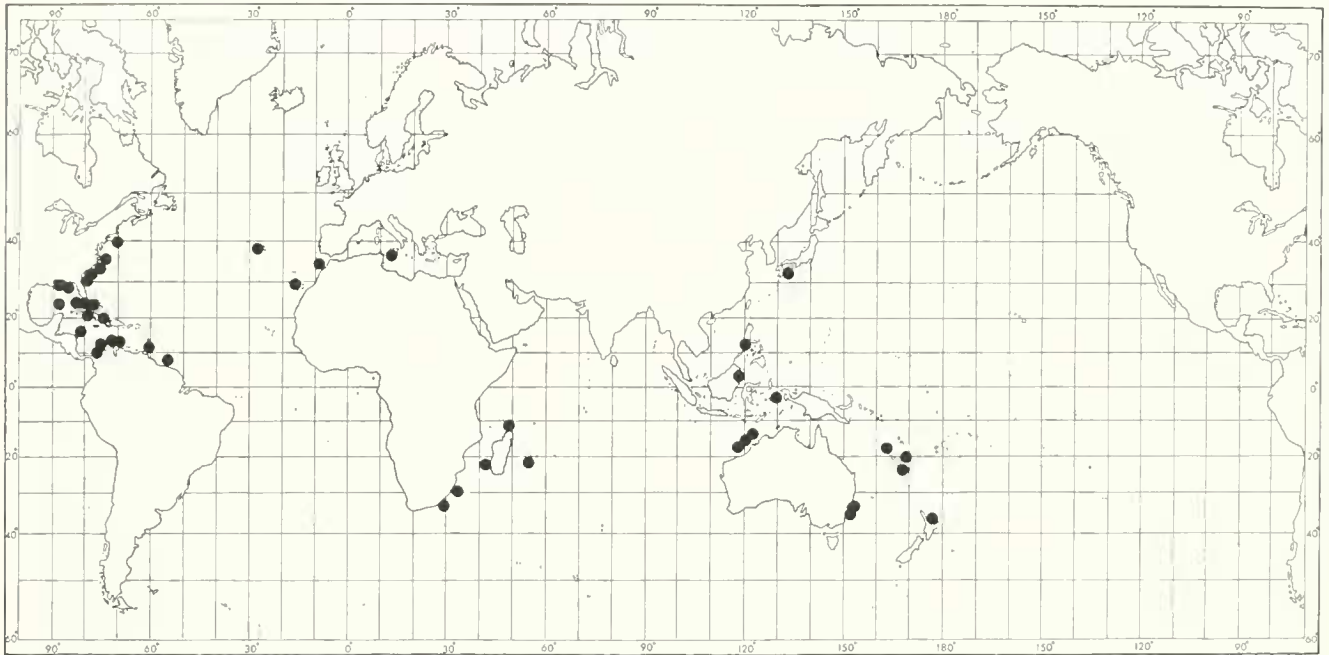


Figure 38. Map showing distribution of *Eudolium bairdii*. Eastern Atlantic distributions provided by P. Bouchet (personal communication).

transported by the Gulf Stream from Western Atlantic populations (see Discussion).

Eudolium crosseanum is closely similar to the Western Pacific and Hawaiian species *E. pyriforme* (see below).

Eudolium crosseanum was the first species described by Monterosato in an illustrious malacological career, and the holotype must have been one of his most prized possessions. He would have been impressed to know that his specimen would still be the only one known from the Mediterranean 122 years after it was described, and that it would remain the largest known example of the species.

Eudolium pyriforme (Sowerby, 1914) (figures 5–8, 21, 27–30, 37)

Dolium pyriforme Sowerby, 1914:37, pl. 2, fig. 14

Eudolium pyriforme.—Osima, 1943:131, pl. 5, fig. 4; Mayblom, 1951:282; Kira, 1959:55, pl. 22, fig. 5; Garrard, 1961:17; Kira, 1962:59, pl. 23, fig. 5; Okutani, 1964:400, pl. 1, fig. 23, text fig. 2; Habe & Kosuge, 1967:66, pl. 25, fig. 12; Kuroda, Habe & Oyama, 1971:135, pl. 37, fig. 4; Wolfe, 1974:3, text fig.; Powell, 1974:201; Cernohorsky, 1976:1, fig. 1; Cernohorsky, 1978:61, pl. 16, fig. 7; Powell, 1979:163; Kosuge, 1985:59, pl. 22, fig. 6; Abbott & Dance, 1986:116, text fig.; Kilburn, 1986:4, fig. 11; Okutani, 1988:78, fig. 46.

Description: *Shell* up to 85.5 (est.) mm high, thin; periostracum thin, translucent, straw-colored. Protoconch yellowish brown; teleoconch sparsely to densely irregularly maculated with pale to deep yellowish brown, major spiral cords alternately spotted yellowish brown and white on a buff white ground, outer lip of many specimens

with a pinkish flush. Protoconch primarily conchiolin, of about 5 convex whorls, 2.95–3.45 mm in diameter, essentially smooth (worn?). Internal calcareous mould not seen. Teleoconch of up to 4.6 evenly convex whorls, sculptured with numerous rounded spiral cords that multiply by intercalation, and fine axial riblets, axials crisp on first 3 whorls, less crisply defined on subsequent whorls, no nodules. Outer lip of most specimens weakly thickened in adults, but a few specimens are moderately thickened and dentate; columella and parietal area simple.

Animal: (figure 21—adult male minus radula that had been extracted when received from one of 7 shells 64–79.5 mm in height, from off Oahu, Hawaii—USNM 804464) externally similar to that of *E. crosseanum* (see above) but differing in that the penis arises nearer outer base of right cephalic tentacle. Jaw similar to that in *E. crosseanum*.

Radula: (figures 27–30—juvenile female 22 mm shell height, Oregon stn. 3636, off Belize City, USNM 751892) similar to that of *E. crosseanum* except that central and lateral teeth have smaller cusps, and sides of central tooth subparallel instead of markedly tapered.

Type data: *Dolium pyriforme*: HOLOTYPE: The Natural History Museum, London 1915.1.6.148, off Kii, Japan.

Other material examined (73 specimens): INDIAN OCEAN—Trawled off Umgababa, Natal, South Africa (1 NMP); trawled off Durban, South Africa, 421 m (1 NMP); trawled off Bazaruto I., Mozambique (1 NMP); 12°39.8'S, 48°16.2'E, N Madagascar, 375–385 m (1 MNHN); 12°42.4'S, 48°14.3'E, N Madagascar, 285–295

m (1 MNHN); 12°42.9'S, 48°12.1'E, N Madagascar, 445–455 m (1 MNHN); 12°43'S, 48°15'E, 300–340 m (1 MNHN); 20°58'S, 55°15'E, off Réunion, 450–580 m (1 MNHN); 22°14.7'S, 43°04.5'E, S Madagascar, 470–475 m (1 MNHN); *Crevettiere* 1986 stn. 80, 22°17'S, 43°04'E, SW Madagascar, 530 m (1 MNHN); *Crevettiere* 1986 stn. 76, 22°22'S, 43°03'E, SW Madagascar, 530 m (2 MNHN); *Crevettiere* 1986 stn. 56, 22°26'S, 43°05'E, SW Madagascar, 435 m (2 MNHN); *Crevettiere* 1986 stn. 57, 22°26'S, 43°06'E, SW Madagascar, 460 m (1 MNHN); *Crevettiere* 1986 stn. 58, 22°26'S, 43°06'E, SW Madagascar, 440 m (1 MNHN); *Soela* stn. 01/84/74, 14°16.5'S, 122°54.4'E, NW of Collier Bay, Western Australia, 302 m (1 WAM); *Soela* stn. 01/84/54, 15°51.2'S, 120°44.3'E, WNW of Lacepede Archipelago, Western Australia, 350–348 m (6 WAM) JAPAN—off Tosa Shimuzu, *ca.* 350–400 m (1 NMNZ); off Ashizuri-misaki (2 MCZ); off Tosa, *ca.* 183 m (1 MCZ); off Kii (1 MCZ). TAIWAN—SW of Taiwan, *ca.* 128–183 m (5 NMNZ). PHILIPPINES—*Albatross* stn. 5289, Batangas Bay, Luzon, 315 m (2 USNM); *Coriolis* MUSORSTOM 3 stn. CP103, of Mindoro, 193–200 m (1 MNHN); *Coriolis* MUSORSTOM 2 stn. CP83, 13°55'N, 120°30'E, off Mindoro, 318–320 m (1 MNHN); Bohol Straits, *ca.* 200 m (5 NMNZ); *Albatross* stn. 5519, off Pt Tagalo, N. Mindanao, 333 m (2 USNM); *Albatross* stn. 5518, off Pt Tagalo, Mindanao, 366 m (2 USNM); 9°43'S, 130°00'E, Timor Sea, *ca.* 250 m (2 NMNZ). HAWAII—*David Starr Jordan* stn. TC-40-54, 21°01.6'N, 156°43.00'W, off Oahu, 223 m (7 USNM). QUEENSLAND and NEW SOUTH WALES—Off Cape Moreton, 165 m (1 AMS); *Kapala* stn. 71-08, *ca.* 32°46'S, 152°16'E, off Newcastle, 280–549 m (1 AMS); *Kapala* stn. K75-05-03, 33°02'S, 152°31'E, off Newcastle, 475 m (1 AMS); between Newcastle and Sydney, 182–549 m (1 AMS); off Broken Bay, 137 m (1 AMS); between Sydney and Norah Head, 412–457 m (1 AMS); *Kapala* stn. K76-07-01, 33°33'S, 151°59'E, off Broken Bay, 384 m (1 AMS); *Kapala* stn. K76-24-05, 33°33'S, 151°59'E, off Broken Bay, 373–366 m (1 AMS); off Sydney, 420–440 m (1 AMS); 35°50'S, 150°34'E, off Batemans Bay, 366 m (1 AMS). CHESTERFIELD REEFS—*Coriolis* MUSORSTOM 5 stn. 376, 19°51'S, 158°30'E, 280 m (1 MNHN). NEW CALEDONIA—*Vauban* MUSORSTOM 4 stn. CP193, 18°56'S, 163°23'E, off d'Entrecasteau Reefs, 415 m (1 MNHN); *Vauban* SMIB 3 stn. DW28, 22°47'S, 167°12'E, 394 m (1 MNHN); *Vauban* SMIB 1 stn. DW2, 22°52'S, 167°13'E, 415 m (1 MNHN); *Vauban* SMIB 2 stn. DW15, 22°53'S, 167°11'E, 375–402 m (1 MNHN); *Vauban* SMIB 2 stn. DW8, 22°54'S, 167°13'E, 435–447 m (1 MNHN); *Vauban* SMIB 2 stn. DW17, 22°55'S, 167°15'E, 428–448 m (1 MNHN). LOYALTY ISLANDS—*Alis* MUSORSTOM 6 stn. DW391, 20°47'S, 167°06'E, off Ouvéa, 390 m (1 MNHN); *Alis* MUSORSTOM 6 stn. CP 465, 21°04'S, 167°32'E, off Lifou, 480 m (1 MNHN). NEW ZEALAND—off Aldermen I., *ca.* 366 m (1 Gardner coll'n, Auckland); BS843 (0.589), 37°14.6'S, 176°51.0'E, Rangatira Knoll, NW of White I., 407–162 m (fragment NMNZ); off Tokomaru Reef, Gisborne, *ca.* 220 m (1 Auckland Institute and Museum).

Distribution (figure 37): Southern Africa, Madagascar, Réunion, Japan, Taiwan, Philippine Islands, Indonesia, Hawaii, Australia, New Caledonia, northern New Zealand; depth range of material examined 137–580 m, deepest known living occurrence 390 m.

Remarks: *Eudolium pyriforme* is extremely similar to *E. crosseanum* in shell color, color pattern, protoconch morphology, shell thickness, size relative to the number of whorls, and in size attained. Although they are also similar in sculpture, *E. pyriforme* differs in having axial riblets that are consistently lower, broader and less sharply defined than those of *E. crosseanum*, especially where traversing the spiral cords. As described above, a single adult male specimen of *E. pyriforme* differs from that of an immature *E. crosseanum* in having the penis base close beside the right cephalic tentacle instead of well behind it (figures 20, 21). The external anatomies of males and females are otherwise similar. Although the position of the penis seems likely to be a major distinguishing feature, with only two different-sized animals for comparison it is impossible to ascertain whether or not its position is infraspecifically stable or changes during ontogeny.

As described and illustrated herein (figures 25–30), the radula of *E. pyriforme* differs from that of *E. crosseanum* in the shape of the central tooth and in the size of the secondary cusps. With only a single radula from each species from dissimilar-sized specimens, however, it is impossible to ascertain either the degree of infraspecific variability at equivalent size, or the degree of morphological change during ontogenetic development (see *E. bairdii* below).

Specimens of *E. pyriforme* tend to be a little narrower than those of *E. crosseanum*, although there is a broad overlap in shape. Shell height/diameter ratio in *E. pyriforme* ranges from 1.41 to 1.72 (mean 1.53, SD 0.095, $n = 30$) as against 1.31–1.66 (mean 1.44, SD 0.085, $n = 18$) in *E. crosseanum*. Specimens from off Hawaii are uniformly narrowly ovate (USNM 804464, height/diameter ratio 1.59–1.72, mean 1.67, SD 0.047, $n = 7$, figure 6). Some specimens from Japan (MCZ 293903), the Timor Sea (NMNZ MF.57428), New South Wales (AMS C.68870) and Mozambique (NMP H.7800) are as narrowly ovate as specimens from Hawaii, however, and there is complete integration between narrow and broad forms in material from west of Hawaii (height/diameter ratio 1.41–1.62, mean 1.48, SD 0.052, $n = 22$).

Eudolium bairdii (Verrill & Smith, 1881)
(figures 10–19, 22, 31–36, 38)

Dolium bairdii Verrill & Smith in Verrill, 1881:299; Verrill, 1882:515; Verrill, 1884:253, pl. 29, figs. 2a,b.

Dolium bayardi (sic.).—Paetel, 1888:221.

Dolium (*Eudolium*) *crosseanum*.—Dall, 1889a:232 (in part), pl. 15, fig. 5.

Dolium (*Eudolium*) *crosseanum*.—Dall, 1889b:134, pl. 15, fig. 5, pl. 44, fig. 2, pl. 62, figs. 83, 83a; Dautzenberg & Fischer, 1906:38 (not *D. crosseanum* Monterosato, 1869).

- Dolium crosseanum*.—Locard, 1897:293 (in part not *D. crosseanum* Monterosato, 1869—*Talisman* stn. 139 record is based on a turrid; P. Bouchet, personal communication).
- Dolium* (*Eudolium*) *crosseanum* var. *solidior* Dautzenberg & Fischer, 1906:35, pl. 3, fig. 1 (*new synonym*).
- Dolium* (*Eudolium*) *crosseanum*.—Kobelt, 1908:155, pl. 126, figs. 2, 3, 4 (in part—fig. 1 = *E. crosseanum*).
- Morio lineata* Schepman, 1909:124, pl. 10, fig. 5 (*new synonym*).
- Eudolium crosseanum*.—Tomlin, 1927:82, fig. 4b; Barnard, 1963:8; Abbott, 1974:168, pl. 6, fig. 1787; Okutani, 1983:264, text fig.; Kilburn, 1986:4, fig. 12; Horikoshi, 1989:63, pl. 15, fig. 11; Warén & Bouchet, 1990:89, figs. 11, 78, 79; Poppe & Goto, 1991:128, pl. 22, figs. 1, 2 (not *D. crosseanum* Monterosato, 1869).
- Eudolium lineatum*.—Osima, 1943:133, pl. 5, fig. 1.
- Oocorys lineata*.—Turner, 1948:178, 190; Abbott & Dance, 1986:116, text fig.
- Eudolium inflatum* Kuroda & Habe, 1952:56 (replacement name for *Eudolium lineatum* Osima not Schepman); Kuroda & Habe, 1957:28, figs. 2, 4, 5; Kira, 1962:59, pl. 23, fig. 4; Okutani, 1988:77, fig. 45; Bieler & Petit, 1990:137 (*new synonym*).
- Eudolium lineatum inflatum*—Kira, 1954:44, pl. 22, fig. 4; Kira, 1959:55, pl. 22.
- Eudolium kuroharai* Azuma, 1960:98, pl. 1, fig. 8, text fig. 1 (*new synonym*).
- Tonna* (*Eudolium*) *crosseana*.—Kilias, 1962:14 (in part).
- Dolium* (*Eudolium*) *crosseanum solida* (sic).—Settepassi, 1971, appendix vii, text figs.
- Tonna* (*Eudolium*) *crosseana*.—Piani, 1977, fig. 11.
- Oocorys solidior*.—Piani, 1977:38, figs. 1, 2, 7.

Description: Shell up to 75.5 mm high, thin to rather thick, periostracum thin, straw-colored. Protoconch deep yellowish to reddish brown; teleoconch white or buff white, major spiral cords yellowish to reddish brown, outer lip white. Protoconch primarily conchiolin, conical, of about 5 convex whorls, 3.00–4.75 mm in diameter, sculptured with 3 narrow spiral threads with small spines (in well preserved specimens). Calcareous mould of inner surface of protoconch (Warén & Bouchet, 1990: fig. 79) similar to that of *E. crosseanum* but with 3 instead of 2 spiral threads. Teleoconch of up to 4.4 evenly convex whorls, sculptured with numerous rounded spiral cords that multiply by intercalation, and fine axial riblets, axials less crisply defined after third whorl, last adult whorl with or without weak to strong nodules on major spiral cords. Shell ranging through intermediates from thin to rather thick. Thin specimens with thin, flared, weakly dentate outer lip and simple columella and parietal area. Most thickened specimens with thick, strongly dentate outer lip, thick spirally plicate callus at base of columella, and 1–3 spirally elongate denticles on parietal area below insertion.

Animal: (figure 22, adult male, shell height 57.5 mm, *Mascareignes III* stn. 24, off Madagascar) externally similar to that of *E. pyriforme*.

Radula: (figures 31–36) (from shells 25, 57 and 76 mm in height) similar to those of *E. crosseanum* and *E. pyriforme*. With increasing size central and lateral teeth

enlarging while size of secondary cusps and area they occupy remain rather static. Secondary cusps ultimately becoming obsolete on laterals in large adults.

Type data: *Dolium bairdii*: HOLOTYPE USNM 51385 (51 × 25 mm), *Fish Hawk* station 945, 39°58'N, 71°13'W, off Barnegat, New Jersey, 379 m; *Dolium* (*Eudolium*) *crosseanum* var. *solidior*: HOLOTYPE Musée Océanographique, Monaco, 38°52.50'N, 27°23.05'W, off the Azores, 599 m; *Morio lineata*: HOLOTYPE Zoological Museum, Amsterdam 3.09.008, *Siboga* stn. 173, 3°27'S, 131°0.5'E, Ceram Sea, 567 m; *Eudolium inflatum*: TYPE MATERIAL (Osima, 1943, pl. 5, fig. 1) possibly in Oshima collection, which was destroyed during World War II (A. Matsukuma, personal communication), off Wakayama Prefecture, Japan; *Eudolium kuroharai*: HOLOTYPE in Mr. M. Azuma's private collection, Takarazuka City, Japan (not seen), off Tosa, Japan.

Other material examined (161 specimens): WESTERN ATLANTIC OCEAN—Barnegat, New Jersey, south to off French Guiana, 39°58'N–7°37'N (12 specimens in 9 lots MCZ, 91 specimens in 43 lots USNM). WESTERN INDIAN OCEAN—12°01'S, 49°26'E, off Madagascar, 450 m, A. Crosnier (1 MNHN); 12°42'S, 48°14'E, off N. Madagascar, 380–375 m, A. Crosnier (1 MNHN); 12°43'S, 48°12'E, off N. Madagascar, 445–455 m, A. Crosnier (1 MNHN); *Marion-Dufresne* cruise 32. stn. CP 144, 20°50'S, 55°35'E, off Réunion, 605–620 m (1 MNHN); *Mascareignes III* stn. 37, 22°18'S, 43°05'E, off S Madagascar (1 MNHN); *Crevettiere* 1986 stn. 80, 22°17'S, 43°04'E, SW Madagascar, 530 m (1 MNHN); *Crevettiere* 1986 stn. 81, 22°23'S, 43°03'E, SW Madagascar, 525 m (2 MNHN); *Mascareignes III* stn. 24, 22°31'S, 43°07'E, off S Madagascar, 430–460 m (1 MNHN); trawled off Umgababa, Natal, South Africa (1 NMP); trawled off Tongaat, Natal, South Africa (1 NMP); off Cape St. Francis, South Africa (1 NMP). WESTERN AUSTRALIA—off Augustus I. south to off Rowley Shoals (2 specimens in 1 lot NMNZ, 23 specimens in 19 lots WAM, 1 specimen USNM). JAPAN—SW of Ashizuri misaki, Kochi Prefecture, trawled (1 MCZ); off Tosa Shimuzu, Kochi Prefecture, 350–400 m (2 NMNZ). PHILIPPINES—*Coriolis* MUSORSTOM 3 stn. CP106, 13°47'N, 120°30'E off Mindoro, 640–668 m (1 MNHN). MALAYSIA—*Albatross* stn. 5592, Sebuku Bay, Borneo, 558 m (1 USNM); *Albatross* stn. 5590, Sebuku Bay, Borneo, 567 m (1 USNM). NEW CALEDONIA—*Vauban* MUSORSTOM 4 stn. DW156, 18°54'S, 163°19'E, Grand Passage, 525 m (1 MNHN); *Vauban* MUSORSTOM 4 stn. DW197, 18°51'S, 163°21'E, Grand Passage, 550 m (1 MNHN); *Vauban* MUSORSTOM 4 stn. CP 171, 18°58'S, 163°14'E, Grand Passage, 425 m (1 MNHN); *Jean-Charcot* BIOCAL stn. DW36, 23°09'S, 167°11'E, 650–680 m (1 MNHN); *Alis* SMIB 4 stn. DW55, 23°21'S, 168°05'E, 215–260 m (1 MNHN). LOYALTY ISLANDS—*Alis* MUSORSTOM 6 stn. CP 467, 21°05'S, 167°32'E, off Lifou, 575 m (1 MNHN). NEW SOUTH WALES—off Port Stephens south to off Brush I. (5 specimens in 5 lots AMS). NEW ZEALAND—N of Mayor I., Bay of Plenty, 380–420 m,

coll. M. Huaki (1 NMNZ); off Aldermen I., New Zealand, 400 m (1 D. Gibbs coll'n, Auckland).

Distribution (figure 38): Atlantic, Mediterranean and Indo-Western Pacific, 17–823 m, deepest known occurrence of living specimen 560 m.

Remarks: *Eudolium bairdii* is rendered highly distinctive by the reddish to yellowish brown spiral bands on the major spiral cords, a pattern in marked contrast to the irregular mottling of *E. crosseanum* and *E. pyriforme*. *Eudolium bairdii* is indistinguishable from the Pacific form that has usually been known as *E. lineatum* (see below). Compared with *E. crosseanum* and *E. pyriforme* at the same stage of growth, the primary spiral cords in *E. bairdii* tend to be more prominent, while the secondary spirals generally enlarge more slowly relative to the primaries. *E. bairdii* differs further in having considerably stronger axial riblets, especially where traversing the spiral cords. The axial riblets in *E. bairdii* tend also to be less crowded, numbering 3–7 per millimeter at the end of the second teleoconch whorl (mean 5.40, SD 1.04, $n = 20$), compared with 6–10 (mean 8.33, SD 1.07, $n = 12$) in *E. crosseanum*, and 6–11 (mean 8.69, SD 1.55, $n = 13$) in *E. pyriforme*. The calcareous internal mould of the protoconch of *E. bairdii* (Warén & Bouchet, 1990: fig. 79—misidentified as *E. crosseanum*) differs from that of *E. crosseanum* (figure 23) in having 3 instead of 2 spiral threads. With only a single protoconch from each species for comparison, however, the degree of infraspecific variability in protoconch morphology is uncertain.

Of the three known living *Eudolium* species, *E. bairdii* exhibits the greatest variation in shell morphology, undoubted adults ranging from 32.5 mm (est.) to 75.5 mm in height, with lightly built or strongly thickened shells, and with or without nodules on the last adult whorl. There is smooth intergradation between all of the extremes both within and between samples from the Atlantic and the Indo-Pacific. By direct comparison of holotypes and topotypes, I am unable to detect any constant differences between *D. bairdii*, *D. crosseanum* var. *solidior*, *M. lineatum*, *E. inflatum* and *E. kuroharai*, and so it is concluded that they are all conspecific. It is significant, however, that thick-shelled forms with heavily thickened outer lips and strongly dentate apertures (extreme *solidior* form) (figures 14, 16) have no strict parallel (figure 17) outside the Atlantic, while specimens from off eastern Australia are thick-shelled and often particularly heavily sculptured, yet they do not exhibit the apertural features of the *solidior* form. These differences suggest that there may have been some genetic drift between isolated, probably largely self-recruiting populations, but these may also be non-genetic responses to local environmental conditions. The latter interpretation is suggested by the fact that a *solidior*-like form is also rarely exhibited by the Atlantic *E. crosseanum* (figure 4) yet not by *E. pyriforme*, its Indo-Pacific sister species. Heavy shelled forms (estimated height 34.5–61.0 mm) are clearly adults and perhaps senescent, and it is

likely that many lightly built forms (32.5–75.5 mm) are also mature. Although type specimens of *D. bairdii* and the synonymized taxa are not illustrated here, illustrations of strongly similar specimens are provided for orientation. *D. bairdii*, *E. inflatum* and *E. kuroharai* (figures 12, 13, 15), *D. crosseanum* var. *solidior* (figures 14, 16), *Morio lineata* (figures 18, 19).

E. bairdii and *E. crosseanum* have fully overlapping geographic and bathymetric ranges in the Atlantic (figures 37, 38), and the two species have been taken together at three stations in the Western Atlantic (*Oregon* stn. 2391, USNM 878126 and 751929 respectively; *Oregon* stn. 4911, USNM 878128 and 751872; *Oregon II* stn. 11253, USNM 766104 and 878129). *E. bairdii* and *E. pyriforme* also have overlapping, geographic and bathymetric ranges and are thus probably locally sympatric.

DISCUSSION

Although larvae of *Eudolium* species have not been observed in the field or reared in the laboratory, the protoconch morphology and species distributions are characteristic of tonnoideans with teleplanic larvae (Scheltema, 1966; Laursen, 1981). Teleplanic larvae remain planktonic for many months, in some species for a year or more, and can be transported great distances in ocean currents (Scheltema, 1966, 1971; Pechenik *et al.*, 1984). Species with teleplanic larvae often have extremely wide amphioceanic, Indo-Pacific, or Indo-Pacific-Atlantic distributions in their benthic stage, especially those with wide tolerances (Scheltema, 1986 and references therein). Although some localities for individuals in the benthic stage do not necessarily support self-recruiting populations, it is clear that widely separated self-recruiting populations are able to maintain their specific integrity through periodic influx of larvae from up-current populations.

Whether or not Eastern Atlantic and Mediterranean specimens respectively of *E. bairdii* and *E. crosseanum* arose from local self-recruiting populations is unknown, but judging from the fact that they are indistinguishable from Western Atlantic specimens and that both species are evidently far more common in the Western Atlantic than in the Mediterranean, it is probable that some if not all originated from Western Atlantic larvae that were transported by the Gulf Stream (Scheltema, 1986). While *E. bairdii* may well be at least partly self-recruiting in the Eastern Atlantic, this is unlikely to be true for *E. crosseanum* in the Mediterranean with a single confirmed specimen. Specific integrity of the strongly isolated Hawaiian population of *E. pyriforme* is probably maintained through intermittent recruitment of larvae from the Western Pacific via the Kuroshio Current (Zinsmeister & Emerson, 1979).

It is likely that the two most closely related species, *E. crosseanum* and *E. pyriforme* originated from disjunct populations of an ancestor that formerly had a continuous distribution in the Tethyan Atlantic-Indo-Pacific. Since *Eudolium* species are unknown living ei-

ther in the Eastern Pacific or from the Western Atlantic south of Columbia, it seems probable that distribution was continuous via Africa rather than America. Unfortunately, the southwestern coast of Africa has been relatively poorly sampled at depths most likely to yield *Eudolium* species (300–600 m) and it is unknown whether or not they occur there. The apparent absence of *E. crosseanum* off South Africa suggests that larvae are incapable of reaching there from northeastern South America in the great counterclockwise South Atlantic gyral. Similarly, larvae of *E. pyriforme* in the warm Agulhas Current are perhaps unable to survive injection into the Atlantic Ocean via the cold Benguela Current. Atlantic and Indian Ocean populations of *E. bairdii* may be fully isolated by the same means. Unless hydrological conditions off southwest Africa were formerly more favorable, perhaps during Pleistocene interglacials, *E. bairdii* and the ancestor of *E. crosseanum* and *E. pyriforme* may have ranged through the circumtropical Tethys Ocean, in which case isolation of eastern and western populations would date from the late Miocene following establishment of the Middle Eastern Landbridge (Por, 1986 and references therein). The second alternative is favored here.

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